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Species abundance distribution and population dynamics in a two-community model of neutral ecology

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Explicit formulas for the steady-state distribution of species in two interconnected communities of arbitrary sizes are derived in the framework of Hubbell's neutral model of biodiversity. Migrations of seeds from both communities as well as mutations in both of them are taken into account. These results generalize those previously obtained for the "island-continent" model and they allow an analysis of the influence of the ratio of the sizes of the two communities on the dominance/diversity equilibrium. Exact expressions for species abundance distributions are deduced from a master equation for the joint probability distribution of species in the two communities. Moreover, an approximate self-consistent solution is derived. It corresponds to a generalization of previous results and it proves to be accurate over a broad range of parameters. The dynamical correlations between the abundances of a species in both communities are also discussed.

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I. INTRODUCTION

An important challenge of community ecology is to explain the observed species abundance distributions (SAD) and their time evolution [1–3]. Hubbell has recently developed an original theory aiming at giving a unified view of biodiversity in communities of trophically similar species such as tropical forests or benthic marine invertebrates [4]. This theory relies on two major drastic assumptions: (i) the community space is permanently saturated (population dynamics is a *"zero-sum game"*); (ii) all individuals in the community, regardless of their species, are strictly equivalent in their ability to survive, to reproduce, to migrate, etc. (*neutrality* hypothesis). This functional equivalence assumption is still a matter of debate [5–10]. Although Hubbell himself acknowledges that "no ecologist would seriously question the existence of niche differences among competing species on the same trophic level" [11], his theory has the great advantage of providing a "zeroth-order approximation" amenable to quantitative predictions with a minimum of input parameters. An excellent review of the mathematical and biological aspects of his theory has been recently reported [12].

The purpose of the present paper is not to discuss the validity of Hubbell's theory, but to report on some new mathematical developments of this model. Recently, several authors have proposed different analytical methods to calculate the species abundance distribution and its time and space evolution [13–18,20–22]. Some questions, however, remain open. In its original version, the model considers the equilibrium between a "community" and a "metacommunity" (the "island-continent" problem). The species abundance distribution in the metacommunity is assumed to be determined by the mutation rate through the "fundamental biodiversity number" θ (essentially the product of the mutation rate by the metacommunity size [4]. On the other hand, the abundance distribution in the community is controlled by the migration rate of seeds from the metacommunity. Implicitly, these approximations rely on the fact that the metacommunity is considered as infinite in size with respect to the community (it acts as a "reservoir" in the thermodynamic sense). A question arises concerning the role played by the ratio of the two community sizes in the dominance/diversity equilibrium. In particular, when one considers the "continuum limit" of the model, both sizes are considered to be infinite and the way the limits are taken becomes crucial [16,22]. Furthermore, the time required to reach equilibrium scales as the community size and it is interesting to study the temporal behavior of two interconnected communities of finite sizes before taking these limits.

We investigate in this paper a model in which the two communities are of arbitrary size and are treated on an equal footing (mutations and migrations in both of them). We show that analytical expressions for the species abundance distributions can be obtained in this more general case and that they are in full agreement with numerical simulations. In addition, we have studied the dynamical aspect of the problem, and some explicit mathematical results are derived for the population dynamics in the two communities.

The paper is organized as follows. We first present the model in Sec. II and its formulation as a master equation (continuous time limit) in Sec. III. Exact expressions concerning the steady-state species abundance distribution are derived in Sec. IV and an approximate self-consistent solution is given in Sec. V. The dynamical correlation of species abundances in the two communities is discussed in Sec. VI and the paper ends by a discussion of the results and of the perspectives of further developments of the theory.

II. THE MODEL

Let us consider two communities A and B with constant overall populations J_A and J_B. Within each of them, the death of an individual is immediately followed by the birth of another one. The new offspring, however, does not necessarily belong to the same species as the dead one. The probability that it actually belongs to the same species is assumed to be proportional to the current abundance of that species.

Mutations (with probability ν) and seed migration (probability m_A from B to A and m_B from A to B) will be taken into account to derive the rate of change of abundance of a particular species in a given community. According to the neutrality hypothesis, the constants ν, m_A, m_B as well as the *per capita* birth and death rates are assumed to be the same for all species. In addition, we assume that the number of mutation-induced variants is so large that any mutation event gives rise to the appearance of a new species.

Considering a species σ of abundance n in A and k in B, the rate of population increase in A, $W_{(n,k)\to(n+1,k)}$, is the product of the probability of the death of a non-σ individual [proportional to (J_A-n)] followed by the birth of an offspring of species σ, arising from the seedling without mutation, of a seed coming either from A [probability $(1-\nu)\times(1-m_A)n/(J_A-1)$] or from B [probability $(1-\nu)m_A k/J_B$]. Taking the individual death rate as unity, one gets

$$\begin{aligned}W_{(n,k)\to(n+1,k)} &= (1-\nu)(J_A-n)\left[(1-m_A)\frac{n}{(J_A-1)}+m_A\frac{k}{J_B}\right]\\ &= A_n(k). \end{aligned}\tag{1}$$

In the same way, the rate of decrease $W_{(n,k)\to(n-1,k)}$ of the population of species σ in A is found to be

$$\begin{aligned}W_{(n,k)\to(n-1,k)} = n\Bigg[&(1-m_A)\frac{(J_A-n)+\nu(n-1)}{(J_A-1)}\\ &+m_A\frac{(J_B-k)+\nu k}{J_B}\Bigg] = C_n(k).\end{aligned}\tag{2}$$

Similar expressions can be written for the rates of population changes in B, $W_{(n,k)\to(n,k+1)}=A'_k(n)$ and $W_{(n,k)\to(n,k-1)}=C'_k(n)$. The coefficients $A'_k(n)$ and $C'_k(n)$ are simply deduced from $A_n(k)$ and $C_n(k)$ by permuting the indices $(A\leftrightarrow B)$ and $(n\leftrightarrow k)$. Note that according to the neutral hypothesis, these coefficients are not indexed by σ, since they are assumed to be the same for all species.

III. THE MASTER EQUATION FORMALISM

A full description of the time evolution of the system requires the calculation of the joint probability $P^{\sigma}_{nk}(t)$ of finding n individuals of species σ in A and k in B at time t. In the continuous time limit, this probability obeys a master equation [16,18],

$$\begin{aligned}\frac{dP^{\sigma}_{nk}}{dt} &= A_{n-1}(k)P^{\sigma}_{n-1,k}+C_{n+1}(k)P^{\sigma}_{n+1,k}-[A_n(k)+C_n(k)]P^{\sigma}_{n,k}\\ &\quad +A'_{k-1}(n)P^{\sigma}_{n,k-1}+C'_{k+1}(n)P^{\sigma}_{n,k+1}-[A'_k(n)+C'_k(n)]P^{\sigma}_{n,k}.\end{aligned}\tag{3}$$

This equation can be written in matricial form by associating the index $q=n+(J_A+1)k$ to the couple of indexes (n,k); P^{σ}_{nk} is then considered as the component P^{σ}_q of a $(J_A+1)(J_B+1)$-dimensional vector $\mathbf{P}^{\sigma}$, which obeys the following differential equation:

$$\frac{d\mathbf{P}^{\sigma}}{dt}=\mathbf{H}\mathbf{P}^{\sigma}.\tag{4}$$

$\mathbf{H}$ is a $(J_A+1)(J_B+1)$-dimensional square matrix that can be expressed as a function of (J_A+1)-dimensional square submatrices $\mathbf{h}(k)$, $\mathbf{u}(k)$, and $\mathbf{v}(k)$,

$$\mathbf{H}=\begin{bmatrix}\mathbf{h}(0) & \mathbf{v}(1) & & & \\ \mathbf{u}(0) & \mathbf{h}(1) & \mathbf{v}(2) & & \\ & \mathbf{u}(1) & \mathbf{h}(2) & . & \\ & & . & . & \mathbf{v}(J_B)\\ & & & \mathbf{u}(J_B-1) & \mathbf{h}(J_B)\end{bmatrix}.\tag{5}$$

$\mathbf{h}(k)$ is tridiagonal and its nonzero matrix elements are

$$h_{mm}(k)=-[A_m(k)+C_m(k)+A'_k(m)+C'_k(m)],\tag{6}$$

$$h_{m,m-1}(k)=A_{m-1}(k),\tag{7}$$

$$h_{m,m+1}(k)=C_{m+1}(k).\tag{8}$$

$\mathbf{u}(k)$ and $\mathbf{v}(k)$ are diagonal matrices defined by

$$u_{mm}(k)=A'_k(m),\tag{9}$$

$$v_{mm}(k)=C'_k(m).\tag{10}$$

The solution of the master equation can be found using the Laplace transform. This technique allows, in principle, not only to find the steady-state behavior of the system but also the transient regime from given initial conditions.

As $\mathbf{H}$ is time-independent, the origin of time can be arbitrarily chosen. We will choose the time origin t_{σ} as the time of appearance of species σ, so that $P^{\sigma}_{nk}(t)=0$ for $t<0$ (if n or $k\neq 0$). It is then possible to define the Laplace transform $\tilde{P}^{\sigma}_{nk}(E)$ of the $P^{\sigma}_{nk}(t)$ and the master equation (4) leads to

$$E\tilde{P}^{\sigma}_{nk}(E)-P^{\sigma}_{nk}(0)=\sum_{m=0}^{J_A}\sum_{j=0}^{J_B}H_{nk,mj}\tilde{P}^{\sigma}_{mj}(E).\tag{11}$$

Introducing the Green matrix $\mathbf{G}(E)=(E\mathbf{I}-\mathbf{H})^{-1}$, the solution of this equation reads

$$\tilde{P}^{\sigma}_{nk}(E)=\sum_{m=0}^{J_A}\sum_{j=0}^{J_B}G_{nk,mj}(E)P^{\sigma}_{mj}(0).\tag{12}$$

Taking the inverse Laplace transform, one then deduces the time dependence of the joint probability distribution,

$$P^{\sigma}_{nk}(t)=\sum_{m=0}^{J_A}\sum_{j=0}^{J_B}U_{nk,mj}(t-t_{\sigma})P^{\sigma}_{mj}(t_{\sigma}),\tag{13}$$

where the evolution matrix $\mathbf{U}(t)$ is the inverse Laplace transform of $\mathbf{G}(E)$. As we assume that species σ appears at time t_{σ} as a single individual either in community A or in community B, $P^{\sigma}_{mj}(t_{\sigma})$ is different from zero only when $(m,j)=(1,0)$ or (0, 1). Therefore, the only elements of the evolution matrix which have to be considered are $U_{nk,10}$ and $U_{nk,01}$. The time dependence of these matrix elements will be discussed in Sec. VI, but, as shown in the next section, their explicit analytical form is not required for the calculation of the steady-state properties of the system.

IV. STEADY-STATE ABUNDANCE DISTRIBUTION IN THE TWO-COMMUNITY SYSTEM

Let $p_n^{I\sigma}(t)$ denote the probability to find species σ with abundance n in community I at time t. The average species abundance distribution $\Phi_n^I(t)$ in that community is the sum of the probabilities $p_n^{I\sigma}(t)$ over all species,

$$\Phi_n^A(t) = \sum_\sigma p_n^{A\sigma}(t) = \sum_\sigma \sum_{k=0}^{J_B} P_{nk}^\sigma(t), \tag{14}$$

$$\Phi_k^B(t) = \sum_\sigma p_n^{B\sigma}(t) = \sum_\sigma \sum_{n=0}^{J_A} P_{nk}^\sigma(t). \tag{15}$$

In the steady state there is a continuous turnover of species, some of them disappearing and others appearing by mutation. Each species σ appears at time t_σ as a single individual either in community A (with probability density νJ_A) or in community B (with probability density νJ_B) so that the joint probability to find an individual of species σ during the time interval dt_σ (i.e., just after apparition of this species) is

$$dP_{nk}^\sigma(t_\sigma) = \nu(J_A\delta_{n,1}\delta_{k,0} + J_B\delta_{n,0}\delta_{k,1})dt_\sigma. \tag{16}$$

As the number of types of variants is assumed to be infinite, a mutant offspring belongs almost certainly to a "new" species that has never been encountered before. Summing over σ in Eqs. (14) and (15) is then just equivalent to summing over t_σ. From Eqs. (13) and (14) one deduces that the steady-state species abundance distribution in A is given by

$$\begin{aligned}\Phi_n^A &= \nu\sum_{k=0}^{J_B}\int_{-\infty}^{t}[J_A U_{nk,10}(t-t_\sigma) + J_B U_{nk,01}(t-t_\sigma)]dt_\sigma \\ &= \nu\sum_{k=0}^{J_B}\int_0^\infty [J_A U_{nk,10}(\tau) + J_B U_{nk,01}(\tau)]d\tau.\end{aligned} \tag{17}$$

The SAD can then be expressed as a function of the Green matrix $\mathbf{G}$,

$$\Phi_n^A = \nu\sum_{k=0}^{J_B}[J_A G_{nk,10}(0_+) + J_B G_{nk,01}(0_+)], \tag{18}$$

$$\Phi_k^B = \nu\sum_{n=0}^{J_A}[J_A G_{nk,10}(0_+) + J_B G_{nk,01}(0_+)]. \tag{19}$$

As $\mathbf{H}$ is a singular matrix, taking the $E\to 0_+$ limit requires some caution. As a matter of fact one can readily show that, in this limit, $G_{00,mj}(E)\to 1/E$ and all the other elements of $\mathbf{G}(E)$ go to finite values.

The problem of the steady-state SAD determination is then reduced to the computation of two matrix elements of the inverse of the $(J_A+1)(J_B+1)$-dimensional square matrix $\mathbf{H}$. Furthermore, this matrix is sparse (the number of its nonzero elements is a linear function of its dimension) so that numerical computation times of the SAD remain short even for values of J_A and J_B of a few hundred (10 s for $J_A=J_B=256$ on a PC).

Typical theoretical SAD are shown in Figs. 1 and 2 for various values of the parameters ν and m_A and for various ratios J_A/J_B [19]. *A priori*, m_A and m_B are independent parameters. A natural choice, however, is to consider that the migration rate is proportional to the size of the community from which seeds migrate ($m_B=m_A J_A/J_B$), and we have adopted this choice in the graphs presented in this paper. Instead of the Φ_n^I, we have found it more convenient to plot the quantities $\omega_n^I=n\Phi_n^I/J_I$, which are normalized,

$$\sum_{n=1}^{J_I}\omega_n^I = 1, \tag{20}$$

and which more clearly show the dominance/diversity equilibrium (ω_n^I represents the probability that an individual randomly drawn from community I belongs to a species of abundance n).

In order to check our theory, we have performed individual based Monte-Carlo numerical simulations (see Appendix A). As shown in Fig. 1, our theoretical predictions are in perfect agreement with the simulations over the whole range of parameters. Numerical simulations, however, require a rather large computation time since averaging over more than 10^5 samples is needed to get an accuracy better than 0.5% for the average SAD. Furthermore, the steady-state regime can only be reached after a number of Monte Carlo steps of order $(J_A+J_B)/\nu$, which limits the possible investigation at not too small mutation rates.

In Fig. 2, typical shapes of ω_n^I curves are shown. According to the input parameters values, four types of behavior are observed: (i) monotonic decrease (large biodiversity), (ii) single broad maximum at small abundances (moderate biodiversity), (iii) flat maximum at small abundance and steep increase at large abundance (coexistence of diversity and dominance trends), and (iv) monotonic increase (dominance).

One can notice that different types of curves may be obtained by changing the ratio J_A/J_B at constant ν and m_A.

Another quantity of interest that can be deduced from the present theory is the "species-area curve." In the present model, the area is proportional to the total population J_I and the number of species S_I is

$$S_I = \sum_{n=1}^{J_I}\phi_n^I. \tag{21}$$

Typical variations of S_A versus J_A or J_B for different values of the mutation and migration rates are shown in Fig. 3. The local abundance increases almost linearly as a function of the local community size J_A when J_A is not small compared to J_B. Various models in the literature suppose that the size of the community B is infinite (island-continent approximation). As we had already pointed out, a relevant question is when the infinity limit can be considered as valid [16]. As it can be seen in Fig. 3(b), the convergence is relatively slow. For the considered set of parameters, the number of species S_A does not show complete saturation up to $J_B/J_A=100$. The community size ratio has to exceed two orders of magnitude for the continent approximation to be valid.

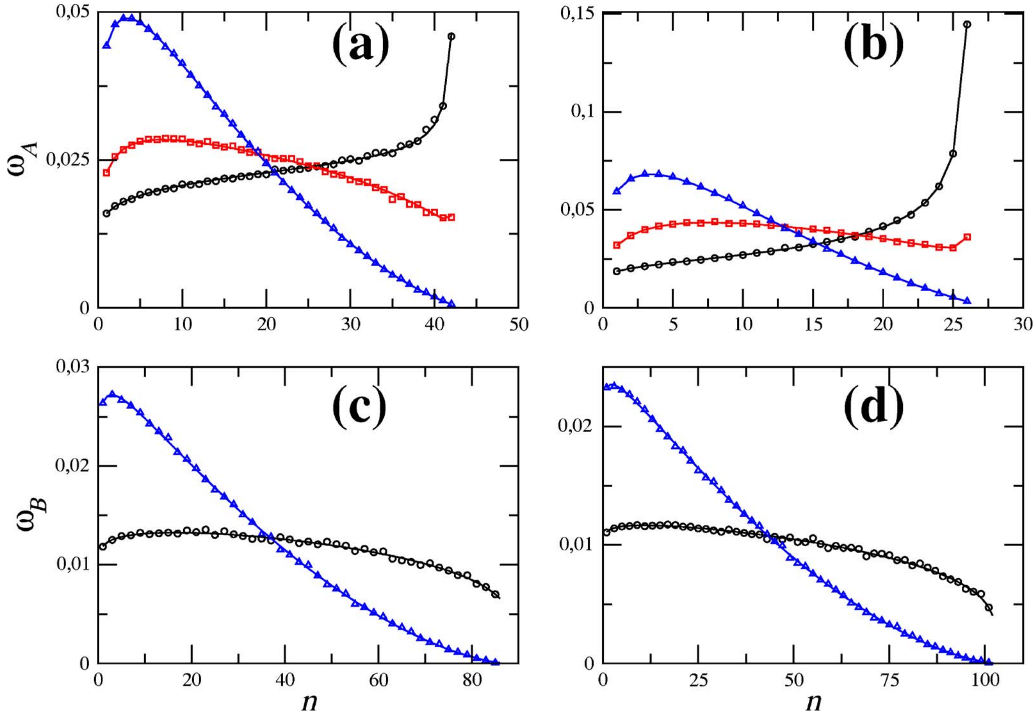

FIG. 1. (Color online) Plot of the normalized distributions ω_I (see text) as a function of abundances. Comparison between exact analytical solution (continuous lines) and individual based Monte Carlo simulations (symbols) for various values of community sizes, mutation, and migration rates. Graphs of the first row (a), (b) are for community A, graphs of the second row (c), (d) for community B. For the first column (a), (c) $J_A=42$; $J_B=86$; for the second one (b), (d) $J_A=26$; $J_B=102$. Black circles: $\nu=0.01$, $m_A=0.02$. Red squares: $\nu=0.01$, $m_A=0.2$. Blue triangles: $\nu=0.02$, $m_A=0.2$.

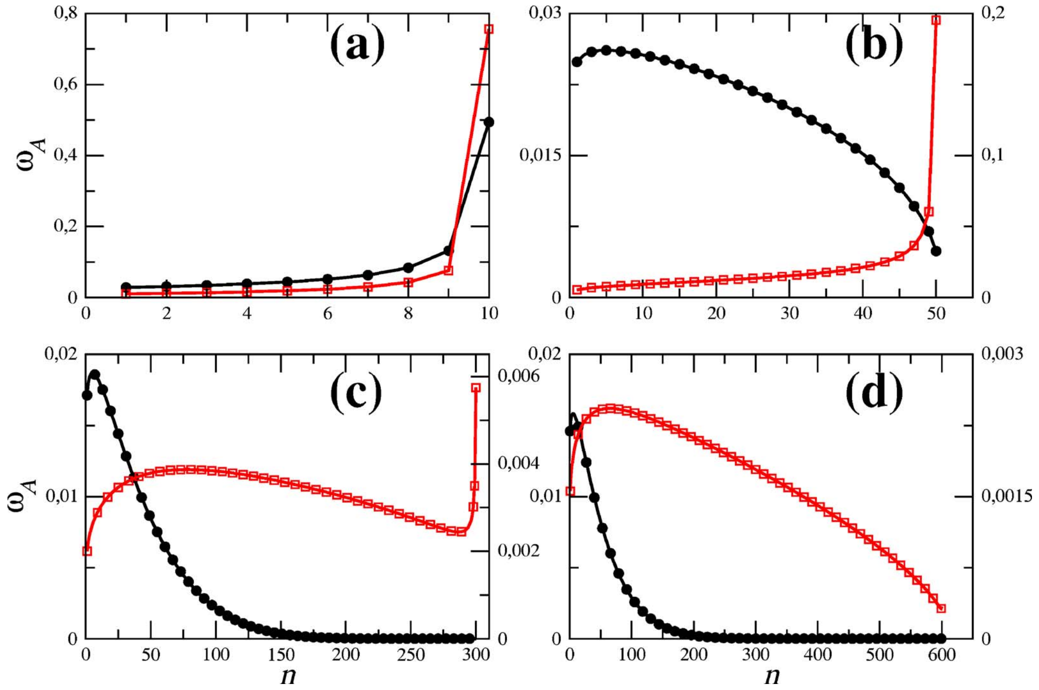

FIG. 2. (Color online) Theoretical normalized distribution of abundances, for various values of A-community size J_A. For clarity, only community A distribution is plotted. In all graphs, $J_B=1000$, $m_A=0.02$. Two values of ν are used in all graphs: black circles, left scale, $\nu=0.01$; red squares, right scale, $\nu=0.001$. (a) $J_A=10$; (b) $J_A=50$; (c) $J_A=300$; (d) $J_A=600$.

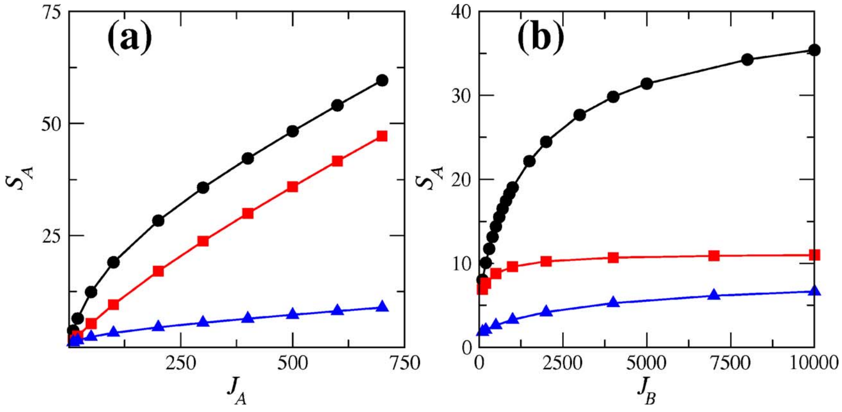

FIG. 3. (Color online) Total number of species S_A as a function of community size J_A (a) and J_B (b) for different migration and mutation rates. Black circles: $\nu=0.01$, $m_A=0.2$; red squares: $\nu=0.01$, $m_A=0.02$; blue triangles: $\nu=0.001$, $m_A=0.02$. (a) $J_B=1000$; (b) $J_A=100$.

V. APPROXIMATE SELF-CONSISTENT SAD CALCULATION

The results described in the preceding section are exact solutions of the master equation and they are valid regardless of the size ratio J_A/J_B. In order to make the bridge with our previous results relative to the "island-continent" model [16], we propose an approximate solution of the master equation that becomes exact at the limit $J_A/J_B \rightarrow 0$ and that provides explicit expression of SAD when the metacommunity is sufficiently large. Indeed, we show that it actually provides a very good approximation for a rather broad range of parameters, even when J_A/J_B is not small.

The approximation we made is of the self-consistent type: The SAD in A is expressed as a function of the SAD in B and *vice versa*. The first step consists of solving the master equation "at constant k," i.e., by calculating the probability $P^{A\sigma}(n;t|k)$ for having n individual of species σ in A at time t, holding at constant k the number of individuals of the same species in B. Note that this is different from the time-dependent conditional probability $P^{A\sigma}(n;t|k;t)$ since it neglects the correlated population changes in the two communities. As shown in Appendix A, in the infinite time limit, one gets

$$P^{A\sigma}(n;\infty|k) = \binom{J_A}{n}\frac{(\mu_A k/J_B)_n[\theta_A + \mu_A(1-k/J_B)]_{J_A-n}}{(\mu_A+\theta_A)_{J_A}} = V^A_{nk}, \tag{22}$$

where $\binom{J}{n}$ denotes a binomial coefficient, $(a)_n = \frac{\Gamma(a+n)}{\Gamma(a)}$ is the Pochhammer symbol, and the coefficients θ_A and μ_A are defined by

$$\theta_A = \frac{\nu(J_A-1)}{(1-\nu)(1-m_A)}, \tag{23}$$

$$\mu_A = \frac{m_A(J_A-1)}{(1-m_A)}. \tag{24}$$

θ_A plays the role of the Hubbell's "fundamental biodiversity parameter," proportional to the mutation rate ν [note however, the additional factor $1/(1-m_A)$ with respect to previous definitions]; μ_A quantifies the dispersal effect (proportional to the migration rate m_A). Using the composition law of probabilities and Eq. (14), the SAD in community A takes the following matricial form (see Appendix B):

$$\mathbf{\Phi}^A = \mathbf{V}^A \cdot \mathbf{\Phi}^B + \mathbf{\Psi}^A, \tag{25}$$

where $\mathbf{\Phi}^A$, $\mathbf{\Phi}^B$, and $\mathbf{\Psi}^A$ are J_A-dimensional vectors and $\mathbf{V}^A$ is a $(J_A \times J_B)$ rectangular matrix with elements V^A_{nk} defined above. The components of the vectors $\mathbf{\Phi}^A$,$\mathbf{\Phi}^B$ are the SAD in A and B, respectively, and the components of the vector $\mathbf{\Psi}^A$ are shown in Appendix B to be given by

$$\Psi^A_n = \frac{\theta_A}{n}\frac{(J_A+1-n)_n}{(J_A+\mu_A+\theta_A-n)_n}. \tag{26}$$

This last term arises from the species that have appeared in A by mutation and have never been present in B.

As both communities are treated on an equal footing, their abundance distributions are related to each other in a symmetrical way and an equation similar to Eq. (25) holds for $\mathbf{\Phi}^B$,

$$\mathbf{\Phi}^B = \mathbf{V}^B \cdot \mathbf{\Phi}^A + \mathbf{\Psi}^B, \tag{27}$$

where $\mathbf{V}^B$ and $\mathbf{\Psi}^B$ have, respectively, the same form as $\mathbf{V}^A$ and $\mathbf{\Psi}^A$ with appropriate permutations of the indexes (A and B) and (n and k).

Equations (25) and (27) represent sets of coupled linear equations and their solutions read

$$\mathbf{\Phi}^A = (\mathbf{1} - \mathbf{V}^A \cdot \mathbf{V}^B)^{-1} \cdot (\mathbf{\Psi}^A + \mathbf{V}^A \cdot \mathbf{\Psi}^B), \tag{28}$$

$$\mathbf{\Phi}^B = (\mathbf{1} - \mathbf{V}^B \cdot \mathbf{V}^A)^{-1} \cdot (\mathbf{\Psi}^B + \mathbf{V}^B \cdot \mathbf{\Psi}^A). \tag{29}$$

These formulas provide an explicit approximate solution of the problem. They generalize our previous results concerning the SAD in the "island-continent" problem: If A designates an island and B a continent, we previously made the simplifying assumptions of neglecting mutations in $A(\mathbf{\Psi}^A=\mathbf{0})$ and migration from A to $B(\mathbf{V}^B=\mathbf{0})$, obtaining the simple results $\mathbf{\Phi}^B=\mathbf{\Psi}^B$ and $\mathbf{\Phi}^A=\mathbf{V}^A\cdot\mathbf{\Psi}^B$.

From Eqs. (25) and (27), one deduces that the ω^I_n defined in Sec. IV takes the following form:

$$\omega^A_n = \frac{1}{\theta_A+\mu_A}\left(\mu_A\sum_{k=1}^{J_B} K^A_{nk}\omega^B_k + \theta_A K^A_{n0}\right), \tag{30}$$

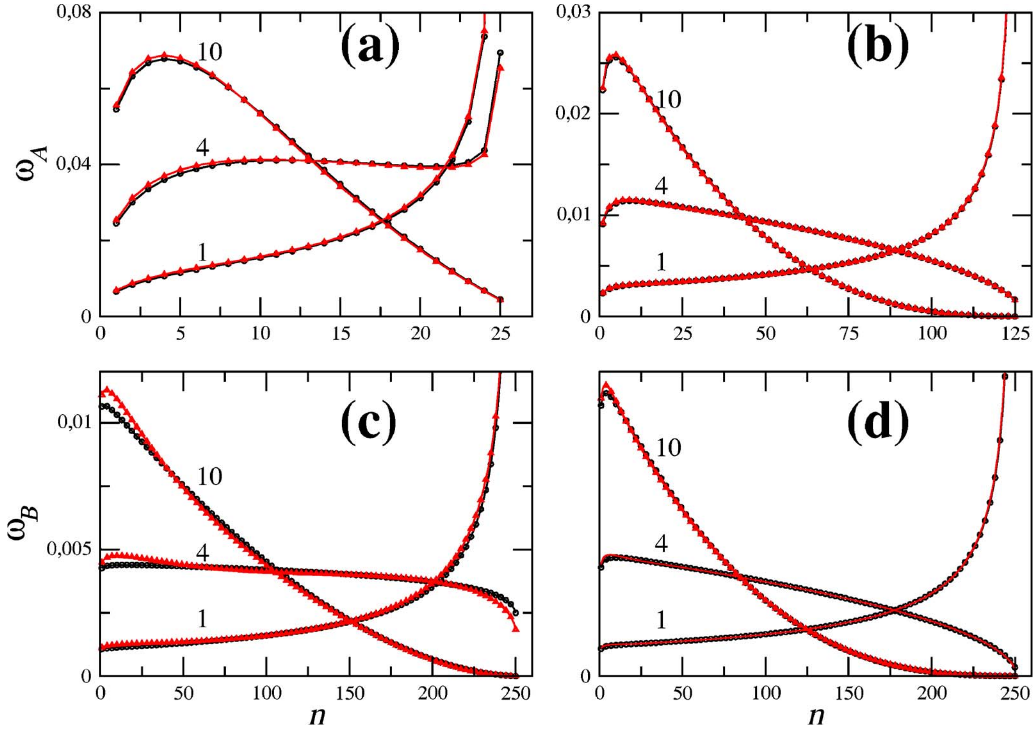

FIG. 4. (Color online) Comparison between the exact and approximate solutions for normalized distribution of species abundances. In all graphs, $J_B=250$, $m_A=0.2$. Black circles designate exact solutions, red triangles approximate ones. First row graphs (a,b) refer to community A, second row graphs (c,d) to community B. In first column graphs (a,c) $J_A=25$; in second column graphs (b,d) $J_A=125$. Each graph contains plots corresponding to three values of ν: 1×10^{-3}, and 4×10^{-3}, 10×10^{-3}.

$$\omega_k^B=\frac{1}{\theta_B+\mu_B}\left(\mu_B\sum_{n=1}^{J_A}K_{kn}^B\omega_n^A+\theta_B K_{k0}^B\right) \tag{31}$$

with

$$K_{nk}^A=\binom{J_A-1}{n-1}\frac{(1+\mu_A k/J_B)_{n-1}(\theta_A+\mu_A-\mu_A k/J_B)_{J_A-n}}{(\theta_A+\mu_A+1)_{J_A-1}}, \tag{32}$$

$$K_{kn}^B=\binom{J_B-1}{k-1}\frac{(1+\mu_B n/J_A)_{k-1}(\theta_B+\mu_B-\mu_B n/J_A)_{J_B-k}}{(\theta_B+\mu_B+1)_{J_B-1}}. \tag{33}$$

Note that, according to Vandermonde's theorem [23],

$$\sum_{n=1}^{J_I}K_{nk}^I=1, \qquad \forall\, k\geqslant 0 \tag{34}$$

so that the ω_n^I defined by Eqs. (30) and (31) actually satisfy the normalization condition Eq. (20). This provides an important check of self-consistency of our approximation.

A comparison between these approximate formulas and the exact ones is shown in Fig. 4 for several values of the parameters ν, m_A, and J_A/J_B.

One can see that the approximation is excellent over a broad range of the parameters. In particular, it is quite accurate for $J_A/J_B\simeq1$ as well as for $J_A/J_B\ll1$. The most important deviations (a few 10^{-2}) are observed for intermediate values of this size ratio ($\simeq0.1$) and especially on the low and high abundance sides of the curves. A practical interest of this approximate theory is to provide explicit analytical SAD expressions [Eqs. (28) and (29)].

VI. DYNAMICAL CORRELATIONS BETWEEN THE TWO COMMUNITIES

The steady state actually corresponds to a constant turnover of species and it is interesting to quantify the population dynamics resulting from mutations and migrations between the two communities. The problem is not trivial because of dynamical correlations between the two communities.

According to Eq. (13), the time evolution of the joint probability distribution $P_{nk}^{\sigma}(t)$ for each species σ requires the knowledge of the evolution matrix $\mathbf{U}(t)$ [or, more precisely, of its matrix elements $U_{nk,10}(t)$ and $U_{nk,01}(t)$]. This can be achieved by diagonalizing the matrix $\mathbf{H}$, expressing the Green matrix $\mathbf{G}(E)$ as a function of its eigenvalues, and taking the inverse Laplace transform of $\mathbf{G}(E)$. The spectrum $\{E_q\}$ of $\mathbf{H}$ is numerically found to be composed of nondegenerate eigenvalues E_q, which range from 0 to $-J=-(J_A+J_B)$,

$$\{E_0=0,E_1=-\nu,E_2=-[\nu+(1-\nu)(m_A+m_B)],\ldots,\\ -(J-2)+E_2,-(J-2)+E_1,-J\}. \tag{35}$$

These eigenvalues correspond to simple poles of the Green matrix, which can then be put into the following form:

$$\mathbf{G}(E) = \sum_q \frac{\gamma_q}{E - E_q}, \tag{36}$$

where γ_q is the matrix of the residues associated to the pole E_q. The evolution matrix is then

$$\mathbf{U}(t) = \sum_q \gamma_q \exp E_q t. \tag{37}$$

No general simple analytical forms can be found for the eigenvalues and the residues, but their numerical computations are straightforward.

Information on the correlated dynamics can also be more simply drawn from the time evolution of the moments of the probability distribution $P^{\sigma}_{nk}(t)$. Starting from Eq. (4), straightforward calculations show that moments of a given order obey differential equations that do not depend on moments of higher order [24]. In the present case, the first moments are found to obey the following simple system of differential equations:

$$\frac{d\langle n\rangle}{dt} = -[\nu + (1-\nu)m_A]\langle n\rangle + (1-\nu)m_B\langle k\rangle, \tag{38}$$

$$\frac{d\langle k\rangle}{dt} = -[\nu + (1-\nu)m_B]\langle k\rangle + (1-\nu)m_A\langle n\rangle. \tag{39}$$

The two eigenfrequencies of the correlated system are $E_1 = -\nu$, which characterizes the decay rate of $(\langle n\rangle + \langle k\rangle)$ (the total average population of the considered species) and $E_2 = -[\nu + (1-\nu)(m_A + m_B)]$, which characterizes the decay rate of $(\langle n\rangle / J_A - \langle k\rangle / J_B)$ (equalization of the relative abundances between the two communities). If $\langle n\rangle_0$ and $\langle k\rangle_0$ denote the initial values of $\langle n\rangle$ and $\langle k\rangle$, the complete solution of Eqs. (38) and (39) reads

$$\langle n\rangle = e^{-\nu t}[J_A(\langle n\rangle_0 + \langle k\rangle_0) + (J_B\langle n\rangle_0 - J_A\langle k\rangle_0)e^{-(1-\nu)(m_A+m_B)t}]/(J_A + J_B), \tag{40}$$

$$\langle k\rangle = e^{-\nu t}[J_B(\langle n\rangle_0 + \langle k\rangle_0) - (J_B\langle n\rangle_0 - J_A\langle k\rangle_0)e^{-(1-\nu)(m_A+m_B)t}]/(J_A + J_B). \tag{41}$$

In the same way, one can show that the second moments are solutions of the following system of differential equations:

$$\frac{d\langle n^2\rangle}{dt} = -2(\lambda_A + \nu/\theta_A)\langle n^2\rangle + 2m_B(1-\nu)(1 - 1/J_A)\langle nk\rangle + (\lambda_A + 2J_A\nu/\theta_A)\langle n\rangle + m_B(1-\nu)\langle k\rangle, \tag{42}$$

$$\frac{d\langle k^2\rangle}{dt} = -2(\lambda_B + \nu/\theta_B)\langle k^2\rangle + 2m_A(1-\nu)(1 - 1/J_B)\langle nk\rangle + (\lambda_B + 2J_B\nu/\theta_B)\langle k\rangle + m_A(1-\nu)\langle n\rangle, \tag{43}$$

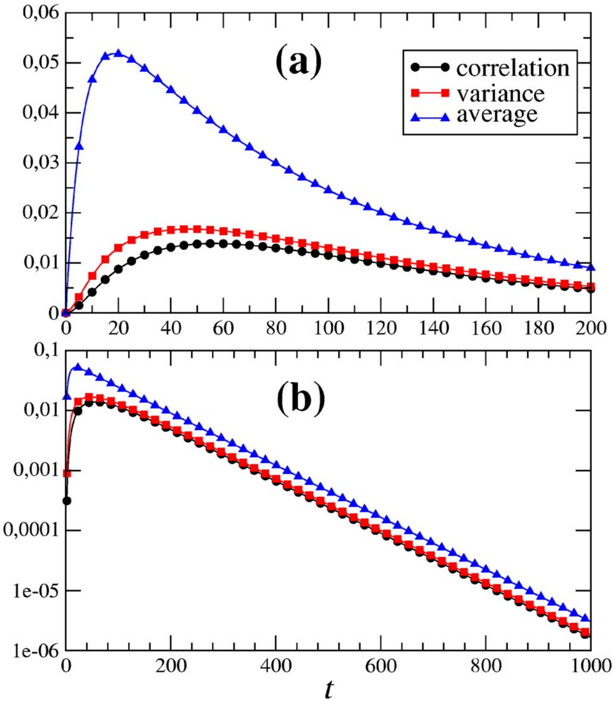

FIG. 5. (Color online) Time evolution of normalized species abundance for average $(\langle n\rangle / J_A)$, variance $[(\langle n^2\rangle - \langle n\rangle^2)/J_A^2]$, and correlation $[(\langle nk\rangle - \langle n\rangle\langle k\rangle)/J_A J_B]$. (a) Short time evolution on a linear scale; (b) long time evolution on a log scale. $J_A = 50$, $J_B = 100$, $\nu = 0.01$, $m_A = 0.1$.

$$\frac{d\langle nk\rangle}{dt} = -(\lambda_A + \lambda_B)\langle nk\rangle + m_A(1-\nu)\langle n^2\rangle + m_B(1-\nu)\langle k^2\rangle \tag{44}$$

with $\lambda_I = [\nu + (1-\nu)m_I]$.

These equations have been numerically solved. The time dependence of the normalized average abundance $\langle n\rangle / J_A$, of the normalized cross correlation $(\langle nk\rangle - \langle n\rangle\langle k\rangle)/J_A J_B$, and of the normalized variance $(\langle n^2\rangle - \langle n\rangle^2)/J_A^2$ are shown in Fig. 5. For an initial condition of the type $P^{\sigma}_{nk}(0) = \delta_{n,0}\delta_{k,k_0}$ (the species under consideration is initially absent in community A and present in B), one finds that the variance and the correlation grow up as t^2 at short times whereas the average abundance in A grows linearly. At long time the three quantities exhibit the same type of decrease proportional to $e^{-\nu t}$ (as a consequence of the extinction of the considered species). Note that the correlation function has its maximum at a time nearly three times larger than the average population.

VII. DISCUSSION

In this paper, we have derived an analytical solution of Hubbell's model of neutral ecology in the case of two interconnected communities of arbitrary sizes J_A and J_B. We have shown that, for some values of the input parameters, original types of SAD are expected that exhibit two maxima corresponding to the coexistence of diversity and dominance trends inside the same community. In the limiting case of a community B much larger than community A, one recovers previous results of the "island-continent" model.

In a recent letter [22], Etienne and Alonso claimed that our expression for the "island" SAD [Eq. (14) in [16]] was "incorrect in the general case" and was only valid in the limit of an infinite metacommunity size. They proposed an alternative formula, called "dispersal limited hypergeometric distribution," which would be "the exact result" for a finite metacommunity size.

We agree that our incriminated formula is only an approximation for finite J_B (it actually corresponds to a limiting case of that derived in the framework of the self-consistent theory described in Sec. V of the present paper). Nevertheless, an essential assumption of the "island-continent" model is that the metacommunity is much bigger than the community: this is the reason for neglecting mutations inside the community and immigration to the metacommunity. Under such conditions (large size ratio J_B/J_A), our formula indeed provides a very good approximation, as is confirmed by a comparison with numerical simulations. On the other hand, it is meaningless to apply this model to the case of a size ratio of order 1 as Etienne and Alonso did when comparing the predictions of both theories (in the lowest graph of their Fig. 1, the community is twice as large as the metacommunity). As soon as the community size ratio becomes finite, self-consistency imposes that both communities be treated on an equal footing, as we have done in the present paper. The exact solution to this more general problem is then shown to be obtained from the master equation formalism.

The interest in this method is not limited to the case of two interconnected "islands;" it can be generalized to the "multi-islands" case. The formalism developed in Secs. III and IV can actually be straightforwardly extended to the case of several communities. In the case of three communities A,B,C, for example, the master equation can be written as in Eq. (4) but the matrix $\mathbf{H}$ is then a square matrix of dimension $(J_A+1)(J_B+1)(J_C+1)$. The SAD in community A is given by a generalization of Eq. (18),

$$\Phi_n^A = \nu\sum_{j=0}^{J_B}\sum_{k=0}^{J_C}[J_A G_{njk,100}(0_+) + J_B G_{njk,010}(0_+) + J_C G_{njk,001}(0_+)]. \tag{45}$$

Obviously, the practical limit is that the size of the matrix $\mathbf{H}$ which has to be inverted to calculate the SAD becomes prohibitively huge when the number of communities increases. Let us note, however, that the matrix $\mathbf{H}$ remains sparse and the number of its nonzero elements increases only as its (linear) dimension. Modeling a small set of interconnected communities of moderate size seems to be a realistic endeavor and it could give valuable information on the steady-state SAD of a spatially extended system in the presence of both mutations and limited dispersal effects (the size of each small "community" would then be the spatial range of seed dispersion).

Another interesting perspective of development of the present theory concerns the time evolution of the SAD between two quasiequilibrium states. If one assumes, for example, that two communities, initially separated, are put into contact at a given time $t=t_0$ (as a consequence of an external environmental event), it would be interesting to describe the transient regime induced by the onset of migrations between the two communities. The master equation formalism provides an attractive starting point to describe such a dynamical process.

APPENDIX A

The Monte Carlo simulation is "individual"-based: Individuals are referred to by their position in an array that contains their species. At each time step, an individual is chosen at random and replaced according to the rules defined in Sec. II.

The communities are thermalized by T rounds of replacements, where $T=6(J_A+J_B)/\nu$ has been found to be a good compromise. After thermalization, abundances are retrieved from the array by sorting the species and counting, for each n, the number of species having exactly n individuals. These abundances are stored in a separate array. The whole process is repeated S times to constitute a statistically significant pool of samples of abundances; the mean abundance is then computed by averaging over these S samples. To get a standard deviation of the mean abundance below 0.5×10^{-2}, we use $S=2\times10^5$. The source code is available upon request.

APPENDIX B

The probability $P^{A\sigma}(n;t|k)$ obeys the differential equation,

$$\frac{dP^{A\sigma}(n;t|k)}{dt} = \sum_{m=0}^{J_A} h'_{nm}(k)P^{A\sigma}(m;t|k), \tag{B1}$$

where $h'_{nm}(k)$ is the matrix $h_{nm}(k)$ with A'_k and C'_k put equal to zero. This equation can be solved using the same Laplace transform methods as in Sec. III. In this case, the eigenvalues E_q^A of the matrix $\mathbf{h}'(k)$ can be explicitly calculated,

$$E_q^A = -q\left[\frac{q-1}{J_A-1}(1-\nu)(1-m_A) + m_A(1-\nu) + \nu\right] \quad (0 \leqslant q \leqslant J_A). \tag{B2}$$

These eigenvalues range from $E_0^A=0$ to $E_{J_A}^A=-J_A$ and, remarkably, do not depend on k. The Green matrix $\mathbf{G}^A(E,k)$ defined by

$$\mathbf{G}^A(E,k) = [E\mathbf{I} - \mathbf{h}'(k)]^{-1} \tag{B3}$$

can then be expanded as a sum of (J_A+1) terms, each of them having a pole at one of the E_q^A,

$$G_{nm}^A(E,k) = \sum_{q=0}^{J_A}\frac{\alpha_{nm}^q(k)}{E-E_q^A}, \tag{B4}$$

where the residues $\alpha_{nm}^q(k)$ can be explicitly calculated from recurrence relations. In particular, the coefficients $\alpha_{nm}^0(k)$ are found to be

$$\alpha_{nm}^0(k) = \binom{J_A}{n}\frac{(\mu_A k/J_B)_n[\theta_A + \mu_A(1-k/J_B)]_{J_A-n}}{(\mu_A+\theta_A)_{J_A}}. \tag{B5}$$

The Laplace transform of $P^{A\sigma}(n;t|k)$ is then

$$\begin{aligned}\tilde{P}^{A\sigma}(n;E|k) &= \sum_{m=0}^{J_A} G^A_{nm}(E,k)P^{A\sigma}(m;0|k)\\ &= \sum_{m=0}^{J_A}\sum_{q=0}^{J_A}\frac{\alpha^q_{nm}(k)}{E-E^A_q}P^{A\sigma}(m;0|k).\end{aligned} \tag{B6}$$

Hence, taking the inverse Laplace transform,

$$P^{A\sigma}(n;t|k) = \sum_{m=0}^{J_A}\sum_{q=0}^{J_A}\alpha^q_{nm}(k)\exp(E^A_q t)P^{A\sigma}(m;0|k). \tag{B7}$$

(In the above expressions, the time $t=0$ corresponds to the time of apparition of species σ *in community* A.)

In the infinite-time limit, the only term that survives on the right-hand side of Eq. (B7) is that corresponding to the mode index $q=0$,

$$P^{A\sigma}(n;\infty|k) = \sum_{m=0}^{J_A}\alpha^0_{nm}(k)P^{A\sigma}(m;0|k). \tag{B8}$$

Since the coefficients $\alpha^0_{nm}(k)$ are independent of the index m (loss of the memory of initial conditions), one gets

$$P^{A\sigma}(n;\infty|k) = \alpha^0_{nm}(k)\sum_{m=0}^{J_A}P^{A\sigma}(m;0|k) = \alpha^0_{nm}(k), \tag{B9}$$

which is Eq. (22).

We then make the hypothesis that the steady-state SAD Φ^A_n can be calculated by considering that $P^{A\sigma}(n;\infty|k)$ obeys the composition law $p^{A\sigma}_n(t) \simeq \sum_{k=0}^{J_B}P^{A\sigma}(n;\infty|k)p^{B\sigma}_k(t)$, in the limit $t\to\infty$ [this is an approximation since $P^{A\sigma}(n;\infty|k)$ is not the true conditional probability]. From Eq. (14), one then deduces

$$\Phi^A_n = \sum_{k=1}^{J_B}\alpha^0_{nm}(k)\Phi^B_k + \Psi^A_n. \tag{B10}$$

The first term corresponds to the contribution of species that have first appeared in community B and have migrated to A. The second term (Ψ^A_n) arises from species that have appeared by mutation in A and have never been present in B. To calculate Ψ^A_n, we use the same reasoning as that leading to Eq. (17) in Sec. IV: one introduces the evolution matrix $\mathbf{U^A}(t)$ defined as the inverse Laplace transform of $\mathbf{G}^A(E,0)$, and one gets

$$\Psi^A_n = J_A\nu\int_{-\infty}^{t}U^A_{n1}(t-t_\sigma)dt_\sigma = J_A\nu\int_0^{\infty}U^A_{n1}(\tau)d\tau \tag{B11}$$

$$= J_A\nu G^A_{n1}(0_+,0) = J_A\nu\frac{A_1(0)A_2(0)\cdots A_{n-1}(0)}{C_1(0)C_2(0)\cdots C_n(0)}. \tag{B12}$$

This last expression has exactly the same form as that previously reported for the metacommunity SAD in the "island-continent" model [16]. When the coefficients $A_n(0)$ and $C_n(0)$ are expressed as functions of θ_A and μ_A, one gets Eq. (26).

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